What is natural?

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PART I - Vectors

Introduced aquatic species of the North Sea coasts and adjacent brackish waters

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Introduction

Introduced aquatic species have received more attention in north-western Europe following the summaries from the German North Sea coast (Gollasch 1996; Nehring & Leuchs 1999), Britain (and Ireland) (Eno *et al.* 1997; Minchin & Eno 2002), Norway (Hopkins 2002) and a more general account for the North Sea (Reise *et al.* 1999). Since then, several inventories have appeared: for the German coast (Nehring 2005), the Dutch coast (Wolff 2005b) and the Danish coast (Jensen & Knudsen 2005). In this account we review, summarize and update all those previous accounts. We have also included non-indigenous introduced species which were known from the North Sea but most probably are extinct in this area today, and species that have been recorded, but for which we have no proof of self-sustaining populations. For the purpose of this account:

- The North Sea is defined from a line between Dover and the Belgian border in the south-west to a parallel line from the Shetland Islands to Norway in the north, and includes the Skagerrak in the east (modified after North Sea Task Force 1993). The boundary between the North- and Baltic Seas, as defined by the Helsinki Commission (www.helcom.fi), is the parallel of the Skaw in the Skagerrak at 57°44.43’N.
- We define marine and brackish-water species as those aquatic species which do not complete their entire life cycle in freshwater (modified after ICES 2005). Marine species are those that have their main distribution in salinities higher than 18 psu; brackish-water species have their main distribution in salinities between 1 and 18 psu.
- Introduced species (= non-indigenous, exotic or alien species) are species transported intentionally or accidentally by a human-mediated vector into habitats outside their native range. Note that secondary introductions may be transported by human-mediated vectors or by natural means (ICES 2005).
- A vector is any living or non-living carrier that transports living organisms intentionally or unintentionally (ICES 2005).

Non-indigenous aquatic species in the North Sea region

In total, 167 introduced and cryptogenic species were reported in the North Sea. There appear to be more records from The Netherlands than from other parts (Fig. 2.1) which may be explained by the most intensive shipping (Port of Rotterdam) and aquaculture (Oosterschelde Estuary) activities in the North Sea region (Wolff 2005b). The lower number of records for the British North Sea coast is more difficult to explain. With respect to red algae, Maggs and Stegenga (1999) suggest that the prevailing alongshore currents from the north are less likely to spread introduced species compared to the eastward currents from Norfolk and the Channel which pass the continental shores of the North Sea.

Figure 2.1 Introduced species in the North Sea region. Pie charts show relative importance of likely introduction vectors for non-indigenous species (excluding cryptogenic species) per country. The total number of non-indigenous species per country is given.

The dominant introduction vectors are shipping and intentional introductions for stocking or aquaculture purposes (Table 2.1, Fig. 2.3). The most recently recorded non-indigenous species are *Rapana venosa* and *Neogobius melanostomus*, which were both recorded for the first time in the North Sea and adjacent waters in 2005 (Kerckhof *et al.* 2006; van Beek 2006). Shortly after the first version of this manuscript was submitted a new non-indigenous species of great concern was found in the North Sea (<2006): *Mnemiopsis leidyi*. This comb jelly was also introduced in other European Seas and contributed to the decline of fisheries.

Table 2.1 Introduced and cryptogenic marine and brackish-water species from the North Sea and distribution records in countries bordering the North Sea. For cryptogenic species, no vector is indicated, and all cryptogenic species are established.. Note added in proof: This table reflects the situation up to March 2006 and only a few remarkable species such as *Mnemiopsis leidyi* and new records of *Urosalpinx cinerea* were added.

Species	Taxonomic group	Country	Status	Habitat	Ballast water	Hull fouling	Aquacult. or stock.	Other	Unknown	Unclear
Coscinodiscus wailesii	Bacillariophyceae	NO SE GE NL BE UK	establ	marine	x		x			x
Chaetoceros calcitrans f. *pumulis*	Bacillariophyceae	UK	uncertain	marine			x			
Odontella sinensis	Bacillariophyceae	NO SE DK GE NL BE UK	establ	marine	x					
Pleurosigma planctonicum (= *simonsenii*)	Bacillariophyceae	NL UK	establ (extinct in NL)	marine	x					
Thalassiosira punctigera	Bacillariophyceae	NO SE GE NL BE UK	establ	marine	x		x			x
Thalassiosira tealata	Bacillariophyceae	NO BE UK	establ	marine	x		x			x
Alexandrium angustitabulatum	Dinophyceae	SE	uncertain	marine	x					
Alexandrium leei	Dinophyceae	NL	establ	marine	x		x			x
Alexandrium minutum	Dinophyceae	NO SE DK	crypto	marine						
Alexandrium tamarense	Dinophyceae	NO SE NL UK	crypto	marine						
Dicroerisma psilonereiella	Dinophyceae	SE	establ	marine	x					
Gyrodinium corallinum	Dinophyceae	SE	establ	marine	x					
Karenia (= *Gymnodinium*) *mikimotoi* (= *aureolum*) (= *Gymnodinium* cf. *nagasakiense*)	Dinophyceae	NO SE DK GE NL BE UK	establ	marine	x					
Prorocentrum minimum	Dinophyceae	SE NL	crypto	marine						
Prorocentrum redfieldii	Dinophyceae	GE NL	crypto	marine						
Thecadinium yashimaense (= *mucosum*)	Dinophyceae	GE	uncertain	marine	x					
Verrucophora cf. *fascima*	Dinophyceae	SE	establ	marine	x					
Chattonella antiqua	Rhaphidophyceae	GE NL	establ	marine	x					
Chattonella marina	Rhaphidophyceae	GE NL	establ	marine	x					
Fibrocapsa japonica	Rhaphidophyceae	GE NL	establ	marine	x					
Heterosigma akashiwo (= *carterae*) (= *Olisthodiscus luteus*)	Rhaphidophyceae	NO NL UK	crypto	marine						
Verruca (= *Chattonella*) cf. *verruculosa*	Rhaphidophyceae	NO SE DK	crypto	marine						
Isochrysis sp. (*Tahitian strain*)	Haptophyte	UK	uncertain	marine			x			
Codium fragile ssp. *atlanticum*	Chlorophyta	NO UK	establ	marine		x				
Codium fragile ssp. *scandinavicum*	Chlorophyta	NO SE DK	establ	marine		x				
Codium fragile ssp. *tomentosoides*	Chlorophyta	NO SE DK GE NL BE UK	establ	marine		x	x			x

Ulva pertusa	Chlorophyta					NL			establ	marine				x	
Acrochaetium densum	Rhodophyta	NO				NL			crypto	marine					
Agardhiella subulata	Rhodophyta					NL			establ	marine	x				
Aglaothamnion halliae	Rhodophyta	NO	SE		GE				establ	marine	x				
Anotrichium furcellatum	Rhodophyta					NL			extinct	marine	x				
Antithamnionella spirographidis	Rhodophyta					NL	BE		establ	marine	x				
Antithamnionella ternifolia	Rhodophyta				GE	NL	BE		establ	marine	x				
Asparagopsis armata	Rhodophyta					NL		UK	establ	marine	x				
Bonnemaisonia hamifera	Rhodophyta	NO	SE	DK	GE			UK	establ	marine	x				
Colaconema dasyae	Rhodophyta					NL			establ	marine	x				
Dasya baillouviana	Rhodophyta	NO	SE	DK	GE	NL			establ	marine	x				
Gracilaria gracilis	Rhodophyta	NO							crypto	marine					
Gracilaria vermiculophylla	Rhodophyta		SE	DK	GE	NL			establ	marine	x				
Grateloupia turuturu (= *doryphora*)	Rhodophyta					NL			establ	marine	x	x			x
Heterosiphonia japonica	Rhodophyta	NO	SE			NL		UK	establ	marine				x	
Mastocarpus stellatus	Rhodophyta			DK	GE				crypto	marine					
Neosiphonia (= *Polysiphonia*) *harveyi*	Rhodophyta	NO	SE	DK	GE	NL	BE	UK	establ	marine	x				
Polysiphonia senticulosa	Rhodophyta					NL	BE		establ	marine		x			
Porphyra miniata	Rhodophyta			DK					establ	marine	x				
Sphaerococcus coronopifolius	Rhodophyta	NO	SE						crypto	marine					
Asperococcus scaber	Phaeophyta					NL			establ	marine	x	x			x
Colpomenia peregrina	Phaeophyta	NO	SE	DK	GE	NL		UK	establ	marine				x	
Elachista sp.	Phaeophyta					NL			establ	marine			x		
Fucus evanescens	Phaeophyta	NO	SE	DK					establ	marine	x				
Laminaria ochotensis	Phaeophyta				GE				uncertain	marine	x				
Leathesia verruculiformis	Phaeophyta					NL			establ	marine	x				
Sargassum muticum	Phaeophyta	NO	SE	DK	GE	NL	BE	UK	establ	marine	x	x			x
Scytosiphon dotyi	Phaeophyta							UK	establ	marine		x			
Undaria pinnatifida	Phaeophyta					NL	BE		establ	marine	x	x			x
Cotula coronopifolia	Anthophyta				GE	NL			establ	brackish				x	
Spartina anglica	Anthophyta				GE	NL	BE	UK	establ	marine			x		
Spartina x townsendii	Anthophyta			DK	GE	NL	BE	UK	establ	marine			x		
Bonamia ostreae	Protozoa					NL			establ	marine		x			
Haplosporidium armoricanum	Protozoa					NL			extinct	marine		x			
Marteilia refringens	Protozoa					NL			extinct	marine		x			
Haliclona (= *Acervochalina*) *loosanoffi*	Porifera				GE	NL			crypto	marine					
Haliclona cf. simplex	Porifera					NL			crypto	marine					
Haliclona rosea	Porifera					NL			crypto	marine					
Hymeniacidon perlevis	Porifera					NL			crypto	marine					
Mycale micracanthoxea	Porifera					NL			crypto	marine					
Scypha scaldiensis	Porifera					NL			crypto	marine					

Species	Taxonomic group	Country							Status	Habitat	Ballast water	Hull fouling	Aquacult. or stock.	Other	Unknown	Unclear
Bougainvillia macloviana	Cnidaria				GE				extinct	marine		x				
Clavopsella (= *Thieliana*) *navis*	Cnidaria				GE	NL			uncertain	brackish		x				
Cordylophora caspia	Cnidaria	NO	SE	DK	GE	NL	BE		crypto	brackish						
Diadumene cincta	Cnidaria				GE	NL			crypto	marine						
Diadumene lineata	Cnidaria				GE	NL		UK	establ	marine		x	x			x
Garveia (= *Bimeria*) *franciscana*	Cnidaria				GE	NL	BE		establ	brackish		x				
Gonionemus vertens	Cnidaria	NO	SE		GE	NL	BE	UK	establ	marine	x	x	x			x
Nemopsis bachei	Cnidaria	NO			GE	NL			establ	brackish	x	x				x
Ostroumovia inkermanica	Cnidaria					NL			extinct	brackish	x	x				x
Rhizogeton nudum	Cnidaria	NO							crypto	marine						
Mnemiopsis leidyi	Ctenophora			DK	GE	NL	BE		establ	brackish	x					
Cercaria sensifera	Trematoda							UK	uncertain	marine			x			
Gyrodactylus salaris	Trematoda	NO							establ	brackish			x			
Pseudobacciger harengulae	Trematoda		SE						establ	marine			x			
Pseudodactylogyrus anguillae	Trematoda	NO		DK					establ	brackish			x			
Pseudodactylogyrus bini	Trematoda	NO							establ	brackish			x			
Anguillicola crassus	Nematoda	NO	SE	DK	GE	NL	BE	UK	establ	marine			x			
Euplana gracilis	Turbellaria					NL			uncertain	brackish		x				
Imogine necopinata	Turbellaria					NL			uncertain	brackish			x			
Stylochus flevensis	Turbellaria					NL			crypto	brackish						
Alkmaria romijni	Polychaeta	NO		DK		NL			crypto	brackish						
Aphelochaeta (= *Tharyx*) *marioni*	Polychaeta				GE	NL			crypto	marine						
Boccardia ligerica (= *Polydora redeki*)	Polychaeta		SE		GE	NL	BE		crypto	brackish						
Clymenella torquata	Polychaeta							UK	uncertain	marine	x	x	x			x
Ficopomatus enigmaticus	Polychaeta				GE	NL	BE	UK	establ	brackish	x	x	x			x
Hydroides elegans	Polychaeta				GE	NL			establ	brackish	x	x				x
Janua brasiliensis	Polychaeta					NL			uncertain	marine		x	x			x
Marenzelleria neglecta	Polychaeta	NO		DK	GE	NL	BE	UK	establ	brackish	x					
Marenzelleria viridis	Polychaeta		SE	DK	GE	NL		UK	establ	brackish	x					
Microphthalmus similis	Polychaeta				GE	NL			crypto	marine						
Proceraea cornuta	Polychaeta					NL			crypto	marine						
Scolelepis cf. *bonnieri*	Polychaeta	NO				NL			establ	marine					x	
Tharyx killariensis	Polychaeta				GE				establ	marine	x	x				x
Tubificoides heterochaetus	Oligochaeta				GE	NL	BE		crypto	brackish						
Corambe obscura (= *batava*)	Gastropoda					NL			extinct	brackish					x	

Crepidula fornicata	Gastropoda	NO	SE	DK	GE	NL	BE	UK	establ	marine			x			
Rapana venosa	Gastropoda					NL		UK	uncertain	marine					x	
Urosalpinx cinerea	Gastropoda					NL		UK	uncertain	marine			x			
Aulacomya ater	Bivalvia							UK	unestabl	marine		x				
Crassostrea gigas	Bivalvia	NO		DK	GE	NL	BE	UK	establ	marine			x			
Crassostrea virginica	Bivalvia				GE	NL		UK	unestabl	marine			x			
Ensis directus (= *americanus*)	Bivalvia	NO	SE	DK	GE	NL	BE	UK	establ	marine	x					
Mercenaria mercenaria	Bivalvia					NL	BE	UK	establ	marine			x	x		x
Mya arenaria	Bivalvia	NO	SE	DK	GE	NL	BE	UK	crypto	marine						
Mytilopsis (= *Congeria*) *leucophaeta*	Bivalvia				GE	NL	BE		establ	brackish	x					
Petricola pholadiformis	Bivalvia	NO	SE	DK	GE	NL	BE	UK	establ	marine			x			
Ruditapes (= *Tapes*) *philippinarum*	Bivalvia	NO						UK	establ	marine			x			
Teredo navalis	Bivalvia	NO	SE	DK	GE	NL	BE	UK	crypto	marine						
Limulus polyphemus	Xiphosura			DK	GE	NL			unestabl	marine					x	
Artemia salina	Branchipoda							UK	unestabl	marine			x			
Eusarsiella zostericola	Ostracoda							UK	establ	brackish			x			
Acartia tonsa	Copepoda		SE	DK	GE	NL	BE	UK	establ	marine	x					
Eurytemora americana	Copepoda					NL		UK	establ	brackish	x					
Myicola ostreae	Copepoda					NL			uncertain	marine			x			
Mytilicola intestinalis	Copepoda			DK	GE	NL		UK	establ	marine		x	x			x
Mytilicola orientalis	Copepoda					NL			establ	marine			x			
Nucellicola holmanae	Copepoda							UK	crypto	marine						
Balanus amphitrite amphitrite	Cirripedia					NL	BE	UK	establ	marine		x				
Balanus eburneus	Cirripedia					NL			uncertain	marine		x				
Balanus improvisus	Cirripedia	NO	SE	DK	GE	NL	BE	UK	crypto	brackish						
Elminius modestus	Cirripedia			DK	GE	NL	BE	UK	establ	marine		x				
Megabalanus coccopoma	Cirripedia					NL	BE		establ	marine		x				
Megabalanus tintinnabulum	Cirripedia						BE		establ	marine		x				
Solidobalanus fallax	Cirripedia	NO					BE	UK	establ	marine		x				
Caprella mutica	Amphipoda	NO			GE	NL	BE	UK	establ	marine	x	x		x		x
Chelicorophium curvispinum	Amphipoda				GE	NL			establ	brackish	x					
Corophium (= *Monocorophium*) *sextonae*	Amphipoda	NO			GE	NL		UK	crypto	marine						
Gammarus tigrinus	Amphipoda		SE		GE	NL			establ	brackish			x			
Incisocalliope aestuarius	Amphipoda					NL	BE		establ	brackish	x					
Melita nitida	Amphipoda					NL			establ	marine	x	x				x
Orchestia cavimana	Amphipoda				GE	NL	BE		establ	brackish	x					
Platorchestia platensis	Amphipoda				GE	NL			crypto	marine						
Callinectes sapidus	Decapoda				GE	NL	BE		establ	marine	x					
Chionoecetes opilio	Decapoda	NO							uncertain	marine					x	
Eriocheir sinensis	Decapoda	NO	SE	DK	GE	NL	BE	UK	establ	marine	x					
Hemigrapsus penicillatus	Decapoda					NL	BE		establ	marine	x	x				x

Species	Taxonomic group	Country							Status	Habitat	Ballast water	Hull fouling	Aquacult. or stock.	Other	Unknown	Unclear
Hemigrapsus sanguineus	Decapoda					NL			uncertain	marine	x	x				x
Homarus americanus	Decapoda	NO						UK	unestabl	marine				x		
Marsupenaeus (= *Penaeus*) *japonicus*	Decapoda	NO							unestabl	marine				x		
Palaemon macrodactylus	Decapoda					NL	BE	UK	establ	marine	x					
Rhithropanopeus harrisii	Decapoda				GE	NL	BE		establ	brackish		x				
Telmatogeton japonicus	Insecta	NO		DK	GE	NL	BE	UK	establ	marine					x	
Bugula simplex	Bryozoa					NL	BE		crypto	marine						
Bugula stolonifera	Bryozoa					NL	BE	UK	crypto	marine						
Smittoidea prolifica	Bryozoa					NL			establ	marine			x			
Tricellaria inopinata	Bryozoa					NL	BE		establ	marine		x				
Victorella pavida	Bryozoa		SE		GE	NL			crypto	marine						
Botrylloides violaceus	Tunicata					NL			establ	marine		x				
Botryllus schlosseri	Tunicata	NO	SE	DK	GE	NL	BE	UK	crypto	marine						
Didemnum sp.	Tunicata					NL			establ	marine					x	
Diplosoma listerianum	Tunicata					NL			crypto	marine						
Molgula manhattensis	Tunicata	NO				NL		UK	crypto	marine						
Styela clava	Tunicata			DK	GE	NL	BE	UK	establ	marine		x	x			x
Lebistes reticulatus	Pisces				GE	NL			establ	brackish			x			
Micropogonias undulatus	Pisces					NL			uncertain	marine	x					
Neogobius melanostomus	Pisces					NL			establ	brackish	x					
Oncorhynchus gorbuscha	Pisces	NO						UK	extinct	marine			x			
Oncorhynchus keta	Pisces	NO						UK	extinct	marine			x			
Oncorhynchus kisutch	Pisces					NL			extinct	marine			x			
Oncorhynchus mykiss (= *Salmo gairdneri*)	Pisces	NO		DK	GE				establ	brackish			x			
Trinectes maculatus (= *Achirus fasciatus*)	Pisces					NL			unestabl	marine	x					

BE = Belgium, DK = Denmark, GE = Germany, NL = The Netherlands, NO = Norway, SE = Sweden and UK = United Kingdom. “Aquaculture” includes species imports for stocking; “hull fouling” includes ships, vessels and pleasure craft; “other” includes ornamental species, species imported for direct human consumption, but released into the wild; “unclear” refers to species for which no single vector could be assigned (in these cases possible vectors are indicated). Key references: Gollasch (1996); Eno *et al.* (1997); Maggs & Stegenga (1999); Reise *et al.* (1999); Wolff (1999); Weidema (2000); Minchin & Eno (2002); Jensen & Knudsen (2005); Nehring (2005); Wolff (2005); Kerckhof *et al.* (2007).

Most introduced species in the North Sea are benthic species, of which most are animal taxa (Table 2.2). More than two thirds of the known introductions have established self-sustaining populations. For others the population status is unknown. For some species there are only single specimen records or occurrences in small numbers and some populations may have been present over varying time periods, although there are no recent records (Fig. 2.2). The majority of introduced species have local distributions (Table 2.3), although 18 taxa were found in six of the seven North Sea countries (i.e. Belgium, Denmark, Germany, The Netherlands, Norway, Sweden and United Kingdom). Many native species are widely distributed on the coasts of North Sea countries and this pattern is generally found for many species that were introduced at an early time and had the ability to become dispersed. Table 2.3 shows that many recent introductions, as well as cryptogenic species, were recorded in one or two North Sea countries, which may indicate a comparatively recent arrival.

Of the total number of introduced species, 136 were marine taxa (81.9%). However, the proportion of marine vs. brackish water invaders varied by country, and marine species dominated. Investigations on alien species will have different levels of effort according to the degree of nuisance a species causes, its size, the available taxonomic expertise and diligence of monitoring surveys in each country. There will almost certainly be other introduced species that have as yet not been recognized. The absence

Table 2.2 Numbers of non-indigenous species in the North Sea per functional group.

Group	Number
Zoobenthos	84
Phytobenthos	36
Phytoplankton	22
Parasite/pathogen	12
Nekton	8
Zooplankton	5
Total	167

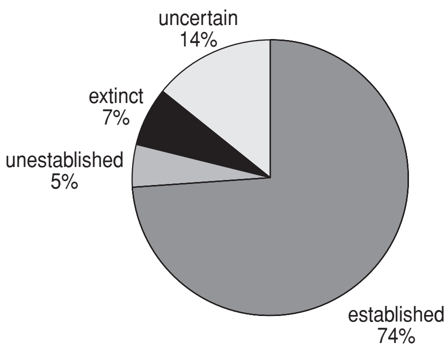

Figure 2.2 Invasion status of non-indigenous and cryptogenic species in the North Sea.

Table 2.3 Occurrence of all non-indigenous and cryptogenic species per number of North Sea countries.

Number of Countries	All non-indigenous species	Cryptogenic species
1	48	11
1	25	11
3	23	8
4	6	3
5	9	
6	8	1
7	10	4
total	129	38

of a species in neighboring countries may reflect some of these issues. For several species, the invasion vector cannot be easily determined, for example, Pacific oysters may be introduced either as adults attached to ship hulls, as larvae carried in ballast water of ships, with imports of stock for aquaculture purposes, or for direct human consumption but released into the environment. We have selected the most likely vector, which in this case we believe to be stock movements of Pacific oysters because the evidence for this is strongest. For species that are most frequently associated with hull fouling, this form of transport was assumed to be the responsible vector. For planktonic taxa and microscopic resting stages we have deemed ballast water to be the most likely vector since such species that are associated with hull fouling might be expected to become flushed away during ship journeys at sea (Table 2.1). The human activities near to the site of the first records generally are assumed to be responsible for an introduction event. However, such deductions are not always secure and for this reason we have indicated where the likely vector remains unclear (Table 2.1, Fig. 2.3).
In summary, the dominant vectors of introductions are shipping-associated vectors (i.e. hull fouling of ships and small craft and ships' ballast water and its sediments) and live aquaculture products, including their associated biota (Fig. 2.3).

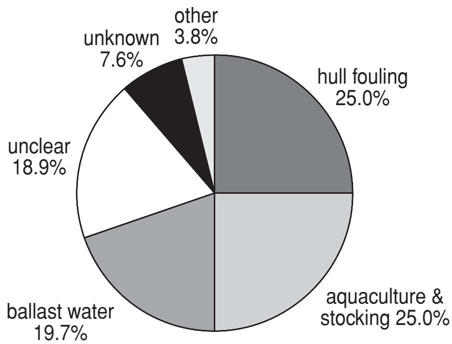

Figure 2.3 Vectors of first introduction for non-indigenous species in the North Sea.

Cryptogenic Species

Some species (n = 38) for which the origin remains unknown or undecided may be identified as introduced species at some future time with, for example, the use of genetic markers. In the meantime these species are deemed to be species of uncertain status, i.e. they are neither demonstrably native nor introduced, and these are assigned to the cryptogenic category (Carlton 1996a). These species may have been introduced during the time of the early sea voyages, and they may have either deliberately or inadvertently become imported to Europe on return from these trans-oceanic voyages. Some of these almost certainly became established and spread within Europe and may today be considered native. The soft-shelled clam *Mya arenaria* is such a species thought to have been introduced to Europe by returning Viking expeditions in the 1200s (Petersen *et al.*1992; Strasser 1999) and the Portuguese oyster *Crassostrea angulata*, may have been carried with returning sailing ships from Taiwan in the 1500s. It is because the study of taxonomy and ecology developed at a later time, from the eighteenth century onwards, that the changes in distributions have been more carefully recorded. During the years preceding ecological and taxonomic studies, ships will have had wooden hulls, which may have been subject to intensive fouling and boring, and they travelled at low speeds and remained immersed in the water over long periods, increasing the possibility of introducing associated species.

There are potentially many overlooked introductions, often belonging to the less conspicuous, and less studied groups, such as interstitial fauna, polychaetes, microalgae, protozoans, hydroids, and bryozoans (Carlton 2003b). Estimating the total number of cryptogenic species in the North Sea is almost impossible, although some indication may be obtained by examining each taxon and its ability to foul or bore in ship hulls or to survive voyages with solid ballast. Indications of a non-indigenous origin may be provided by identifying species with disjunct distributions, low dispersal potential, high fouling capacity and the likelihood of interacting with a human mediated vector and route that may have occurred at some point in time.

Non-indigenous species recorded in the North Sea as a result of natural dispersal

In the introduction, an overview was given of the published accounts of introduced species in the North Sea region. These accounts tend to list only those species that have known impacts or are commonly encountered. Species recorded as non-indigenous in these country reports may actually be native to another North Sea country, or to the biogeographic region encompassing the North Sea and may have spread by human activities. Natural events, such as exceptional water inflow due to rare hydrodynamic events or storms, can result in (mostly) temporary occurrence of species outside their normal ranges (e.g. Berge *et al.* 2005). Vagrant species such as fishes (i.e. *Mola mola* and *Carcharinus longimanus*), neustonic species (i.e. *Lepas anatifera*) and planktonic species occasionally appear in the North Sea under such natural circumstances. Wiltshire (pers. comm.) and Franke & Gutow (2004) have indicated that many species newly found in the North Sea previously had eastern distribution limits in the British Channel, but these have been extended into the North Sea in recent decades most probably due to climate change (Stachowicz *et al.* 2002; Beare *et al.* 2004; Perry *et al.* 2005). Some species native to warmer climate regimes have colonized lagoons or docks that generally have higher temperatures, or appear in some areas in summer or in areas where there are thermal plumes. For example, the polychaete *Ficopomatus enigmaticus* was first recorded at the London Docks (United Kingdom) in 1922 (Eno *et al.* 1997), in the port of Vlissingen (The Netherlands) in 1967 near a power plant (Wolff 2005b) and also in the port of Emden (Germany) in close proximity to a power plant (Kühl 1977). Today, the species is widespread in the south-western North Sea and is established in four countries (Belgium, Germany, The Netherlands and The United Kingdom).

Case Histories

Three introduced species that have a significant impact in the North Sea and are found in all seven countries are selected as case studies. These are the slipper limpet *Crepidula fornicata*, the Chinese mitten crab *Eriocheir sinensis* and the shipworm *Teredo navalis*. These species have varying social, economic and ecological effects within the North Sea region.

Crepidula fornicata – the Slipper Limpet

This snail has a thin white shelf inside the shell aperture that protects the visceral mass, giving it a slipper-like appearance and it can attain a size of 5 cm. Individuals are most often found in a 'chain' with the oldest, female individual at the base. Following its planktonic phase the crawling male seeks to attach to the last member of a chain where it will remain confined. Over time the male gradually transforms to a female to which other wandering males may become attached to extend the chain to as many as twelve individuals. Those that do not find chains may self-fertilize (Cole 1952). In temperate waters *C. fornicata* can produce more than one brood a year and survive up to ten years. This species is a successful invader because of its persistent recruitment success and ability to colonize a wide range of habitats. Its first known occurrence in Europe was in 1872 in Liverpool Bay, England. It did not form an established population at this time but did so at a later time on the south-east coast of Britain following introductions of half-grown American oysters *Crassostrea virginica* relaid on estuarine shores.

Once introduced, a population can develop to nuisance levels within ten years. *C. fornicata* is tolerant of a wide range of conditions within its native range where it occurs from the Gulf of St Lawrence to northern Mexico. It occurs in shallow bays, estuaries and lagoons where temperatures range from –6°C when exposed to frosts to

>25°C, and salinities of 25–35 psu, but it can endure short periods of lower salinity (Walne 1956). Should mortalities arise from extreme weather events, recruitment from planktonic larvae can take place from deeper waters. There is evidence that slipper limpet populations declined during cold winter periods (Thieltges *et al.* 2004). However, the current trend of warmer winters may have aided in its continued northward expansion. It now occurs as far north as 59°N on the Norwegian coast but has also extended its range southwards to the Spanish rias. For some reason it has not become abundant in the shallow Baie de Arcachon in France (Montaudouin *et al.* 2001). *C. fornicata* is also known to occur in Sicily in the Mediterranean Sea.

The routes and modes of spread of the slipper limpet are varied. It reached Europe tucked with American oysters inside wooden barrels dispatched as deck cargo on steam-ships from Long Island Sound (Minchin *et al.* 1995). These oysters were laid on shores and the limpets among them colonized an estuary on the southeast coast of Britain, first found there in 1893. It then spread, partly aided by its planktonic larval stage, to become established along the south British coast. It has also been spread with flotsam. Specimens were stranded on Belgian shores in 1911 and soon after became established there. Korringa (1942) found many specimens attached to a stranded wreckage on the Dutch coast in 1926. A few years later the species was found in the Oosterschelde estuary; in 1930 it had become common. On 'D-Day' in 1944 during the Second World War, large numbers of *C. fornicata* were carried to Normandy, France, as hull fouling on the undersides of Mulberry Harbors used to deliver military equipment ashore. These floating units had acquired sufficient limpet fouling while awaiting deployment in sheltered British estuaries (Blanchard 1997).

Much of the slipper limpet expansion along North Sea coasts has involved the movement of oysters between estuaries and lagoons such as the Wadden Sea (Thieltges *et al.* 2003) and the Limfjord. It has even spread to isolated islands such as Helgoland. Scallops often bear the slipper limpet and stocking with sowing sized scallops may also result in its secondary spread.

Off the coast of Brittany, this limpet has become associated with maerl deposits which are important for conservation. In some areas, such as Marennes-Oleron, *C. fornicata* populations are culled by dredging to reduce their competition with oysters (Deslous-Paoli 1985). Abundant slipper limpets change sediment structure by the accumulation of vast numbers of their vacant shells and fine particles from faeces and pseudofaeces accumulated within these shells. In the 1980s, *C. fornicata*'s biomass in Europe probably exceeded one million tonnes (Quiniou & Blanchard 1987). Although during the Second World War 4000 tonnes of *C. fornicata* were processed for human consumption, it has not been marketed since.

Soon after its arrival in Europe it was declared an 'oyster pest', although the evidence is somewhat equivocal. In field experiments, Montaudouin *et al.* (1999) could not find any effect on the growth of the Pacific oyster *Crassostrea gigas*, and by use of carbon and nitrogen isotopes, Riera *et al.* (2002) found differences in food sources; however, competition was shown between the slipper limpet and the mussel *Mytilus edulis*. Thieltges (2005a) found negative effects of the slipper limpet on mussel growth and survival. However, mussels with attached slipper limpets were also found to have higher survival rates than mussels without slipper limpets, which suffered from higher levels of predation by sea-stars (Thieltges 2005b). Chauvaud *et al.* (2000) have suggested that the impact of harmful algal blooms can be reduced where the slipper limpet is abundant. Apparently, there is a complex series of interactions within an ecosystem that results in both negative and positive effects of this invader on other components of the ecosystem (Thieltges *et al.* 2006).

Outside of Europe, *C. fornicata* occurs on the North American Pacific coast, Japan and Uruguay. It has the ability to colonize other temperate estuaries and inlets of the world, such as on the southern coastline of Australia, Tasmania and New Zealand, South Africa and South America. It is possible that it is distributed to these regions by oyster transports or as hull fouling on ships. Vigilance in the monitoring of oyster transports should aid in preventing their establishment in these regions.

In areas where *C. fornicata* has become abundant, individuals or some small chains were first found. Early reporting, if soon acted on, may thus lead to elimination. Following the 1993 European Trade agreement, the Pacific oyster, subject to some conditions, may be transported within European waters. This is likely to lead to the further spread of the slipper limpet and of other species unless consignments are carefully monitored. Despite management measures, the high dispersal ability of the slipper limpet has ensured that it spread within Europe following its establishment over a century ago. This spread has been due to the variety of vectors it is associated with, but also to natural spread of larvae and settled stages. The eastern oyster drill *Urosalpinx cinerea*, native to the northwest Atlantic coast, was introduced along with the slipper limpet to the south-east coast of Britain at about the same time. This predatory snail has no pelagic life-history stage, which reduces its natural dispersal potential. The close regulation of the movement of oysters in Britain from the areas where it occurs and the prevention of its spread within Europe even after a century appeared to demonstrate that some control measures do work. However, *U. cinerea* was recently introduced to The Netherlands with mussel imports from the United Kingdom and Ireland and appears to have established in the Oosterschelde estuary (Faasse & Ligthart 2007; 2009).

Eriocheir sinensis – *the Chinese Mitten Crab*

This crab's life-cycle is characterized by migration between waters of different salinities. Larvae develop in marine waters and juveniles and young adults actively migrate upstream into freshwater habitats. Two-year-old adults migrate downstream to marine conditions, which may take several months and during this they become reproductively mature. There is no native crab in Europe with a similar catadromous mode of life. *E. sinensis*'s area of origin are waters in temperate and tropical regions between Vladivostock (Russia) and southern China (Peters 1933; Panning 1938). The centre of occurrence is the Yellow Sea, a temperate region off northern China (Panning 1952). The mitten crab was first recorded outside its native range in 1912 in the German river Aller. It has been suggested that *E. sinensis* was introduced to Germany with ballast water. In Europe, it is most abundant in estuaries adjacent to the North Sea. The first mass development was documented during the 1930s – and was followed by other mass occurrences in the 1940s, 1950s, 1980s and 1990s (Schnakenbeck 1924; Boettger 1933; Sukopp & Brande 1984; Anger 1990; Reise 1991; Michaelis & Reise 1994; Clark *et al.* 1998; Fladung pers. comm.). After the last mass occurrence the crab population declined in Germany (Strauch pers. comm.). Soon after it was first found, it spread to the Baltic coast of Germany (1926) and Poland (1928), probably via the Kiel Canal. Today it is frequently found along southern and eastern Baltic coasts up to the eastern Gulf of Finland. This is >1500 km from the German Bight, its main centre of abundance (Ojaveer *et al.* 2007). While it seems unlikely that self-sustaining populations occur in the central and eastern Baltic due to low salinities, which are unsuitable for larval development, an egg-carrying female was recently found in Lithuanian waters at very low salinity (Olenin pers. comm.). Other records of the crab in Europe are from the White Sea, Norway, Ireland, Portugal, Black and Caspian Seas, and even the French Mediterranean coast without any indication of establishment. Mitten crabs also invaded other regions of the world. They were first found in San Francisco Bay in 1992 and have since spread up and down the coast (Cohen & Carlton 1995; Rudnick *et al.* 2000). Individuals were collected in the Great Lakes from 1965 to 1994 (Nepszy & Leach 1973) and from Quebec, in the St Lawrence River (de Lafontaine 2005). A single Chinese mitten crab was collected in the Mississippi River delta in 1987 (Felder pers. comm.).

When abundant, there is considerable impact. The mitten crab preys on native species, fishes caught in traps and nets, and cultured fishes in ponds. It also has habitat structuring effects, mainly by burrowing in river embankments, causing erosion and damage to dikes. Crabs also aggregate on water-intake filters of industrial cooling water supplies and drinking water plants.

In its native range in Asia, the Chinese mitten crab is the second intermediate host for the human lung fluke parasite. The oriental lung fluke is a parasite which uses a snail as its primary host, freshwater crayfish and crabs as intermediate hosts, and a variety of mammals (including humans) as the final hosts. The fluke settles in the lungs and other parts of the body, and can cause severe bronchial illness (Ichiki *et al.* 1989). The disease is not known in Europe, but it may become established in the future.

Since its first occurrence in 1912, the crab's economic impact in Germany is estimated at €80 million (based on modified calculations of Fladung pers. comm.). These costs include catchment gear installation and maintenance, impact on bank erosion and loss in commercial fisheries and pond-aquaculture (estuaries and in-land). Chinese mitten crabs can be marketed at €1–3 per kg for industrial use and for direct human consumption on the Asian markets. During 1994–2004, crabs to the total value of approximately €3–4.5 million were sold in Germany (Gollasch & Rosenthal 2006). However, this is still much less than the costs of mitigation.

***Teredo navalis* – the Shipworm**

The description of *Teredo navalis* by Linnaeus in 1758 was based on material collected by Sellius in The Netherlands in 1730–1732. Its massive occurrence during these years

(Vrolik *et al.* 1860; Van Benthem Jutting 1943) suggests a non-indigenous origin. Mass occurrences have often been observed for non-indigenous species some years after their introduction and in several cases this resulted in their discovery (e.g. Ostenfeld 1908).

The classical authors Aristotle, Ovid, and Pliny (Vrolik *et al.* 1860), living by the Mediterranean Sea, knew of shipworms, but the species involved are not known. Almost a thousand years later, from 1516 onwards, shipworms were reported from the West Indies and Atlantic Europe (Moll 1914). Vrolik *et al.* (1860) record fossil finds from northwest Europe, but it is unclear whether these are of Holocene age and belong to this species. Moll (1914) lists only fossil finds belonging to other species. There seem to be no records of damage to Viking vessels in northern Europe (Hoppe 2002). However, in the historical museum of Haithabu (Germany), wood with boreholes from the stem of a Viking ship is on display (Minchin pers. obs.). Since this vessel was found in a freshwater environment, later colonization by marine borers can be excluded. It is unclear, however, which species created these boreholes. The first confirmed accounts of *T. navalis* in Atlantic Europe are from The Netherlands.

Van Benthem Jutting (1943) states that, before 1730, *T. navalis* occurred sporadically along the Dutch coast. She refers to Hooft (1580) who recorded damage to seawalls in Zeeland, but without identifying the cause (Moll 1914). Vrolik *et al.* (1860) cite the 'Journal des Savants de l'an 1665' and state that vessels in the IJ estuary at Amsterdam were virtually destroyed by the shipworm (however, this may be due to a different species, e.g. *Psiloteredo megotara* or *Teredo norvegica*, and the "worms" may have colonized the ships elsewhere). Martinet (1778) also records heavy damage to herring fishing vessels in 1714 and 1727. Any records before 1730 concern either unspecified damage or the occurrence of shipworms in vessels. Hence, it seems that until the eighteenth century we have no clear indication that *T. navalis* occurred in wooden structures in The Netherlands. In 1730 considerable damage to wooden constructions along seawalls was recorded from Zeeland and West-Friesland in The Netherlands (van Benthem Jutting 1943). Vrolik *et al.* (1860) record damage to seawalls in 1730, 1731, 1732, 1770, 1827, 1858 and 1859, and found a relationship between the outbreaks of *Teredo* and dry, warm summers and periods of higher salinities. In the eighteenth century, however, its occurrence in the wood constructions protecting Dutch seawalls was considered a disaster which enforced a radical and costly switch to new dike protection methods. The former wooden poles at the seaward side of the dike had to be replaced by stones imported from abroad. In the eighteenth and nineteenth century, damage to the wooden tide gates and locks was also widespread in The Netherlands and Germany. In The Netherlands a special governmental 'shipworm committee' was even installed to study causes of the problem and suggest solutions (Vrolik *et al.* 1860). The construction of the German naval base at Wilhelmshaven was seriously delayed when a protective dam constructed out of parallel pilings with earth in between them was damaged by a shipworm infestation and collapsed during a storm in January 1860 (Blackbourn 2006). Thereafter the occurrence of *Teredo* gradually declined because wood was no longer used for commercial ship building and dike construction and more resistant tropical hardwoods were being used for the doors of locks.

Recently, *T. navalis* showed up for the first time in the brackish waters of Bremerhaven in the Weser estuary, where it was most abundant in fir floating fenders (>10,000 m^2) but less abundant in fir and oak pier posts (Tuente *et al.* 2002). It is also common in Dutch coastal waters today (Wolff 2005b) and is apparently increasing in wooden coastal defense structures in the northern Wadden Sea (Reise pers. obs.). Elsewhere in the North Sea *T. navalis* still causes minor economic damage occurring in driftwood, wrecks, and wooden poles.

Van Benthem Jutting (1943) considers *T. navalis* to be a cosmopolitan species probably originating from the North Sea area, whereas eighteenth-century authors believed that ships returning from the East Indies were responsible for their introduction (e.g. Martinet 1778). However, during this period, North Sea states were trading worldwide and *T. navalis* may have been introduced from anywhere. It is for these reasons that this species is considered to be cryptogenic.

Conclusions

We presented a checklist of 167 non-indigenous and cryptogenic species in the North Sea. Shipping associated and aquaculture vectors are considered to be the dominant vectors. More than two thirds of the recorded non-indigenous species have established self-sustaining populations. The majority of non-indigenous species have localized distributions; only ten of these are known from all of the seven countries bordering the North Sea.

Crepidula fornicata, Eriocheir sinensis and *Teredo navalis* are examples of non-indigenous and cryptogenic species that have a significant impact on coastal systems of the North Sea. Reise *et al.* (1999) concluded that in the North Sea introduced species in most cases increase biodiversity without having major unwanted economic or ecological impacts. However, nowadays the introduced Pacific oyster *Crassostrea gigas* is spreading in the coastal waters of the North Sea (Reise *et al.* 2005) and is replacing the native blue mussel *Mytilus edulis*. This rapid spread is probably promoted by the recent warm summers which support the recruitment of the Pacific oyster (Diederich *et al.* 2005) and also due to the lack of cold winters which are required for good recruitment of *M. edulis*. It is assumed that the current abundance of *C. gigas* may become reduced should water temperatures decline (Nehls *et al.* 2006). However, this is unlikely because of a continuing trend of rising seawater temperatures in the region.

In the North Sea region paleoenvironmental history as well as strongly transformed modern coastal environments have contributed to a relatively low species richness. Many of the species that were introduced and tolerated the physical regime became established, increased local diversity and together considerably modified ecosystem functioning in the nearshore zone (Reise *et al.* 2006).

Plants like the introduced cordgrass *Spartina anglica* and the Japanese seaweed *Sargassum muticum* altered structural complexity, while abundant benthic filter feeders like the molluscs *Ensis directus*, *Crassostrea gigas* and *Crepidula fornicata* can be assumed to impact regional plankton dynamics in the coastal waters. Some introduced species have the capability of re-organizing trophic relationships within an ecosystem and influencing economies both negatively and positively. Though potentially enormous, the impacts of introduced species are highly unpredictable. Those with noted impact in other temperate regions are likely to have impact in the North Sea. Others may develop unexpectedly high levels of abundance or cause disease and harm that could not be predicted. Since ballast water can carry millions of propagules which are being discharged into North Sea harbors each day, and because other vectors may further spread these species, we need an improved understanding of the vector mechanisms involved in order to reduce unwanted species introductions in the future.

The rate of invasions has increased in the North Sea (Reise *et al.* 1999), as it has increased worldwide, and it will probably continue to increase as a consequence of climate change and globalization. For each individual species, the potential number of transport vectors has also increased, e.g. the European shore crab *Carcinus maenas* is potentially dispersed by ten different vectors today, whereas 200 years ago there were two possible modes of transport and dispersal (Carlton & Cohen 2003).

Knowledge of the invasion process is essential in designing management plans to cope with the potential detrimental effects of invasive species, and to attempt to prevent their large-scale spread. The checklist of introduced species in the North Sea provided here can serve as a basis for future studies of introduced species and design of management plans in this region, but as the list will inevitably continue to grow longer, it will need to be periodically updated.